Neglected Quaternary legacy of biodiversity for the Mountains of Southwest China

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Abstract

Mountains of Southwest China (MSWC) is a biodiversity hotspot with very unique and highly complex terrain. With the majority of studies focusing on the biogeographic consequences of massive mountain building, the Quaternary legacy of biodiversity for the MSWC has long been overlooked. Here, we took a comparative phylogeography approach to examine factors that shaped community-wide diversification. With data from 30 vertebrate species and the results reveal spatially concordant phylogeographic structure, indicating riverine barriers are an important proxy for illustrating phylogeographic history, and temporally clustered divergence events during severe glacial cycles. We conclude that the repeated glacial cycles and the heterogeneous montane environments have left a unique phylogeographic imprint in the MSWC. The orderly process of diversifications unravels profound implications for conservation and calls for further comparative phylogeographic investigations in this biodiversity hotspot.

Keywords: comparative phylogeography, Mountains of Southwest China, Pleistocene diversification, riverine barrier, species pump, full-likelihood Bayesian computation

Introduction

Although the uplift of mountains and the associated impact on diversification is widely recognized, including for the Mountains of Southwest China (MSWC), the processes associated with this complex topography and associated barriers as recent drivers of divergence remain relatively less studied. This is especially the case for the MSWC, one of the most topographically complex and species-rich biodiversity hotspots (1). In the past two decades, researchers conducted hundreds of biogeographic and phylogeographic studies in MSWC to study the vicariance events associated with the uplifting of Tibetan Plateau, such as the separation between Asian catfish genera (2), and between Senecioneae genera (3). Yet, many cryptic species and recent speciation events have been discovered and documented in this region (4-8), and the divergence events dated clearly after major orogenesis events in this region (4, 7), suggesting an

important role for recent divergence in generating the biodiversity in this region, and that mechanisms other than geographic events should be considered.

we currently only have limited information on recent diversification events and the mechanisms—those responsible for population differentiations and cryptic speciations—in MSWC. On the temporal scale, these events typically concentrate in the Pleistocene (2.0Ma–150ka) (9). Spatially, species often exhibit discrete genetic patterns that correspond to geographic or ecological barriers to dispersal, such as arid-hot valleys, basins, or icy mountain tops (10). Most studies only recognize the whole MSWC region as an east-west dispersal barrier; yet, MSWC itself is a piece of extremely rugged terrain—three major rivers (the Salween, Mekong, and Yangtze) divided this area from west to east in order (Figure 1), forming deep-cutting canyons that are at least 2,000 m lower than the mountain ridges on the two sides. Hence, on finer geographic scale, do populations of different species have concordant spatial structure? Similarly, on finer temporal scale, are these divergences between populations synchronized? Were the divergence time determined by species-specific bio-trait characteristics (e.g., habitat preference), or past spatiotemporal processes affecting the whole community? The rivers had similar contributions, or each played a distinct role? These questions remain to be answered.

Here, we adopted a community-wide approach to decipher the phylogeographic pattern across multiple co-distributed species in the MSWC. The concordance of spatial structures and the temporal synchronization of divergences across species within the MSWC community could be used to test hypotheses about mechanisms that generated biodiversity (11-13). Specifically, we analyze data sets from previous phylogeographic studies conducted in the MSWC (Table S1 in Supplementary file 1), as well as generated new sequencing data for some mammal species (Table S2 in Supplementary file 1), and tests for concordance of species phylogeographic structure using a full-likelihood Bayesian computation method (FBC) to test community-wide phylogeographic hypotheses. For all non-flying terrestrial animals in this study, genetic data reveals that at least one of the rivers functioned as dispersal barriers — many species have

spatially concordant phylogeographic structure. Hence, we more specifically tested three hypotheses with different levels of temporal synchronization among spatially concordant species: asynchronous hypothesis (H1) in which taxa have independent divergence histories; synchronous hypothesis (H2) in which all taxa "share" one co-divergent event; and partially synchronous hypothesis (H3) in which taxa grouped into more than one co-divergence events (Figure 2). We aim to: (i) to test whether there are prevailing phylogeographic histories among co-distributed species in MSWC; and (ii) to explore factors that contributed to the community-wide phylogeographic diversity in MSWC.

Results

Data acquisition

We took the *sensu lato* concept of the MSWC, geographically broader than the biodiversity hotspot MSWC (10). We surveyed the Web of Science using the keyword 'phylogeog*' and 'China,' and only kept studies that are in our focus area (Figure 1) and have georeferenced genetic data. To study the role of the river barriers in generating genetic diversity, we chose species spanning at least one river. Together with our newly sequenced data for six mammal species, we compiled a dataset of 2278 mitochondrial sequences from 30 terrestrial species (14 small mammals, 10 birds, and 6 amphibians or reptiles; Table S1). All these species are typical members of MSWC animal community.

Examining the spatial phylogeographic structure

We used the mitochondrial gene tree estimated by BEAST v2 (Bouckaert et al., 2014) to examine whether river barriers correspond to monophyletic clades on the gene tree (Figure S1–S3, Supplementary file 2). These clades were also confirmed by species delimitation analysis using GMYC (14). Rivers correspond to phylogeographic breaks in all examined mammal species: few clades are found on both sides of a river (Figure S1–S3). Depending on the whole species range, the number of phylogeographic divisions ranges from one to three (Figure 3). All

amphibian/reptilian taxa also show conspicuous within-species genetic divergence — species have at least one phylogeographic split; two have an even subtle pattern with three clusters identified (Figure 3). However, populations were less explicitly structured than that in mammals as more monophyletic clades are distributed across rivers. Among the bird taxa, six of the ten species did not show evident population structure; for the four species that exhibited a phylogeographic division, in two species there was no geographic structure (i.e., the mitochondrial clades overlap geographically).

With regards to phylogeographic structure associated with the different rivers, the Mekong river contributes more than the other two in shaping the phylogeographic diversity of the MSWC animal community (Figure 3): specifically, 14 phylogeographic divisions associated with the Mekong (12 of which are in mammals), 7 with the Salween (4 in mammals), and 8 with the Yangtze (6 in mammals). However, there is not a significant association between particular taxonomic groups and specific river barriers (paired t-test, $p > 0.05$; Figure 3).

Testing community-wide co-divergence in time

Using the estimated gene trees, the deep divisions were used to define lineages; in some cases, the lineages correspond to proposed subspecies, or even disputed species boundaries. Given the taxonomic status of these lineages defined by the clades do not affect the time estimates of divergence events, we hereafter refer to them as clades, and our analysis focus on the divergent time between clade pairs, which total to 33 divergence events (Figure 3).

For individual clade pair, we used two programs, BEAST (15) and BPP (16), to estimate the split time of individual clade pairs. Overall, divergence time estimates in BEAST had higher variance than that in BPP (Table S2), but the median values were close (Figure S4, Supplementary file 2). The estimated split time of mammalian clades spans from 0.44 to 1.50 Ma; the split time in amphibians and reptiles are between 0.57 and 0.83 Ma, with the single exception of an older split at 1.93 Ma in the Yunnan pond frog (*Babina pleuraden*; Figure 3). In contrast, the divergence

time in birds was much more variable: the youngest was 0.30 Ma while the oldest dated back to 2.30 Ma (Figure 3; Table S2). From the perspective of each of the river barriers, divergence events are largely overlapping, and clearly do not support a single divergence event for all species in the community (Salween: 0.45–1.21 Ma; Mekong: 0.49–1.93 Ma; Yangtze: 0.44–1.50 Ma; Figure 3).

To test co-divergence across species, we chose the FBC method implemented in ecoevolity (17) instead of other ABC methods based on summary statistics. Relying on insufficient summary statistics inevitably discards some information in the data, and the chosen summary statistics might be insufficient (18). FBC takes full advantage of sequence information by calculating the likelihood of the population divergence model directly from genetic data while analytically integrating all possible genealogical and mutational histories. Compared to hABC (19), this method is less sensitive to priors and less biased towards co-divergence events (17). In addition, simulation using empirically derived parameters showed that the FBC outperforms hABC with single-locus data (Jamie Oaks in prep.), and therefore we focus exclusively on the results based on FBC analyses.

We first ran FBC with all the taxa pairs multiple times with different priors on the concentration parameter of the Dirichlet process. Because of the lack of clear geographic barrier, we excluded the bird species from this comparative analysis, leaving twenty-nine mammalian, amphibian, and reptilian clade pairs. There is no posterior support for total synchronous divergence (Bayes factor <1), suggesting that the diversification at the MSWC is a complicated history. For the number of co-divergent event, 14–19 co-divergence events have highest posterior support but with considerable uncertainty — the posterior distribution is very flat and no posterior probability is larger than 0.18 (Table S3, Supplementary file 1), so the estimated number should be treated with caution. We found that clade pairs sharing the same geographic barrier (i.e., river) do not have more overlap of their posterior distribution of estimated divergence time. The mean overlap percentage between two clade pairs at the same river is 12%, 18% and 7% for the Mekong,

Salween, and Yangtze, respectively, while those at different rivers on average overlap 18% (Figure S4). That is, two species sharing a geographic barrier are not more likely to have similar divergence time.

Given this lack of temporal and spatial correlation, we conducted separated FBC runs for each river to examine whether the divergence events at each river were totally asynchronous. The results clearly show support for limited numbers of co-divergence events (Table 1 and Figure 4). FBC run on the Yangtze river supported three co-divergence events (PP = 0.55, 2lnBF = 18.28; Figure 4), and both the Mekong (PP = 0.52, 2lnBF > 27.82) and Salween river (PP = 0.91, 2lnBF = 23.55) supported two events (Figure 4). There is almost no posterior support for totally synchronous divergence (Bayes factor <1; Figure 4). Thus, the partially synchronous hypothesis (H3) gained the highest support in these analyses (Table 1). Overall, rivers have one old diversification — around 0.5Ma for the Salween and Yangtze and 0.85Ma for the Mekong river, and one or two very recent diversification pulse between 0.1–0.2 Ma. This explains why the overall correlation between the temporal and spatial scale is not significant, but suggests that species in the MSWC community do not have completely idiosyncratic histories.

Discussion

In the past two decades, more than two hundred molecular phylogenetic/phylogeographic studies were conducted to study the evolution of biodiversity in the MSWC (20). Our study is the first to assess community-wide shared phylogeographic patterns in MSWC terrestrial animals. Combing data from multiple species under one model-based analysis not only increases the accuracy of divergent time estimates but also can statistically test whether there are prevailing evolutionary histories in the community. All the non-flying animals included in our analysis have deep genealogical splits corresponding to at least one of the rivers (Figure S3). This concordant spatial structure suggests that rivers in the MSWC are effective isolation barriers for these animals. We also found the divergence events are partially synchronous (hypothesis H3 in Figure 2) — each river only has a limited number of pulses of co-divergence events, and all of them occurred

during the mid to late Pleistocene (with 67% between 0.5–1.0 Ma; Figure 3). It supports a strong signal of the Pleistocene "species pump" effect. Nevertheless, despite dozens of glacial cycles in this era, the divergences only happened during severe glaciations (e.g., S1, S2, S5, S7 by Chinese Loess Sequence; MIS6, MIS8, MIS12, MIS22 by Marine Isotope Stages). This spatially concordance and partial temporal synchronicity implies a unique diversification mechanism, which, we believe, results from a combination of the riverine barrier effect and the mountains' drastic variation in topography acting as buffer against mild climate changes (see below).

Diversification in the MSWC as a result of geographic features and past climate event

Climate oscillations in Pleistocene have long been known as an effective speciation mechanism in mountainous regions (21, 22). Species range shifts during the Pleistocene could lead to isolation (e.g., isolation between different refugia) or gene flow (e.g., sky island dwellers moved down to the valley forming one population). Hence it is not surprising that phylogeographic studies on organisms in other mountains system (e.g., the Alps in Europe and Madrean Sky Island mountain ranges in North America) usually reveal deep genealogical splits possibly representing different refugia populations, and the estimated divergent time often fall within the Pleistocene (23, 24). However, the genealogical clades often lack obvious or concordant geographic structure as we observed in the MSWC (10). As water-bound distributions are common for terrestrial species (and their phylogeographic lineages), the rivers in the MSWC that acted as dispersal barrier for the community (birds are the exception) are crucial in generating a spatially concordant phylogeographic pattern.

On the other hand, the mountains in the MSWC, we think, contribute to the partially synchronous divergent history. These mountains are north-south oriented, and all have altitudinal zonation spanning from tundra to tropical forests. Both features are very rare in the world and made the MSWC an ecosystem with substantial stability. In moderate glacial cycles, the majority of the MSWC species only have to migrate vertically or slightly southward to track climate change (25), given that the species richness concentrates at the mid elevations (26-28). Even if

these animals reach the bottom of the mountains, the rivers can still prevent gene flow between different populations. That is, the environmental gradients in the MSWC act as a buffer and the rivers as barriers to secondary contact (9). Only dramatic glaciations that shift species distribution further south (Figure 5), can create opportunities for connectivity and isolation between populations. Under this scenario, the divergence time between current populations are predicted to cluster with the severe glaciation events, which is consistent with our results. In contrast, in Amazon, another biodiversity hotspot, rivers have flatter drainage and also define the boundary for many primates (29) and bird species/subspecies (30), but taxon pairs of birds divided by two vast rivers, Rio Negro and Rio Branco, have chiefly asynchronous divergence history (30). The extremely rugged terrain and rivers made the impact of glaciations on species community more punctuated in the MSWC.

The importance of studying recent diversification in MSWC

Understanding the mechanism of recent diversifications is indispensable for understanding how biodiversity was generated and maintained in the MSWC. Divergence events in MSWC has an extended time range, even for phylogeographic divisions within species. For example, phylogeographic divergences in subnival plants across the Mekong–Salween Divide — a classic biogeographic boundary, also known as the Ward Line — varied from late Pleistocene (0.37–0.48 Ma) (31) to the Pliocene (4.49 Ma) (32). Mosbrugger et al. (9) recently reviewed the Cenozoic evolution of geobiodiversity in the general Tibeto-Himalayan region and pointed out the three peaks of diversification: the first flourishing of modern families and genera during the mid□Miocene (20–15Ma), the second during the Miocene-Pliocene boundary, and the third, the focus of our study, at the early and mid-Pleistocene (2.0Ma–150ka).

However, the mechanisms behind the most recent peak of diversification are often overlooked. One main reason is that the MSWC is adjunct to Tibeto-Himalayan region, the third pole of the earth. Majority of the phylogeographic studies in this region have aimed to find the footprint of the orogenesis process on biodiversity. Many studies reported young divergence events (2.0 Ma–

150ka), but were “mired” by this “uplift story”, and falsely ascribed them to orogenesis processes. Only recently, careful reviews of geographic evidences questioned the often-cited literature on the third uplift phase of Tibetan Plateau (15–0.5 Ma) (20), and the current geographic consensus is that the orogeny in this region finished long before the Pleistocene. This leaves very few studies recognizing and investigating the effect of Pleistocene climate change on species diversity in the MSWC.

Studying recent divergence (i.e. phylogeographic processes) in the MSWC is also difficult, yet crucial for conservation. Many taxa in this region have taxonomic ambiguity. In fact, more than half of our studied species are cryptic species recognized in recent, and many are still in species complexes. MSWC is a crucial region for conservation—over 30% of plant species (~12,000 species), and about 50% vertebrates (~1,100 species) of China live here (according to the Catalogue of Life China 2019 Annual Checklist), including many endangered species. Characterizing this cryptic diversity—how they distribute spatially and how climate change might affect them—is important for comprehensive conservation planning in the MSWC (33, 34).

Future directions

Our study provided unprecedented insight for MSWC’s often-neglected recent diversification process on both spatial and temporal scales. One drawback due to the availability of published data is that we only used mitochondrial loci in the analysis. Because of the stochastic nature of gene coalescence, mitochondrial-only data sets often cannot give accurate estimates of divergence time. However, our analysis was based on a "community" single-locus dataset, which gains statistical power by "borrowing strength" across taxa. Moreover, we applied a recently developed method—FBC—to extract more information from genealogical history (17). Nevertheless, potential problems, such as matrilineal inheritance and mutation-rate difference, still exist. Nowadays, applications of genomic data in phylogeographic studies (e.g., RAD-seq) are growing (35), and have been successful in revealing biogeographic barriers (36) and forecasting the impact of climatic changes (37). Recent research on Philippine geckos used

genomic data to detect differences among population divergences within very narrow time intervals (17).

Future studies should also consider expanding the taxon sampling — the number of species falling into each co-divergence pulses are still small. More taxa would allow us explore the possible connection between biological traits and divergence pulses. Harnessing the power of high-throughput sequencing data and larger-scale sampling of species in the community would be a promising approach to further our understanding of recent diversification mechanisms in the MSWC.

Conclusion

With complex terrain, mountains harbor a substantial proportion of the world's species. This disproportionately high species richness, as well as the mechanisms of evolutionary diversification, have long intrigued biologists (38, 39). With the help of comparative phylogeographic methods, our study explored the fascinating phylogeographic diversity harbored in the MSWC and our result suggest a unique mechanism generating diversity through the Pleistocene. Despite the complexity of the MSWC system and the limited amount of data, the overall of phylogeographic pattern is apparent: limited pulses of synchronous divergence during severe glacial cycles. These findings are consistent with a complex biogeographic process resulted from the interaction of Pleistocene's species pump effect and the extremely rugged terrain of the MSWC. Future studies in the MSWC with genomic-scale data and more species sampling would further our understanding of the mountain biodiversity evolution across space and time.

Materials and Methods

The dataset included mitochondrial DNA (mtDNA) data from 24 species collected from GenBank (see Table S1 for the original studies). The present study also sequenced the Cytb gene in six mammal species (Genbank no. XXX-XXX).

Matrilineal phylogeographic structure and divergence time estimation for individual species

We analyze the phylogeographic breaks for each species in two steps. First, we estimated a gene tree using BEAST v.2 (15). If the original paper did not specify, we used a lognormally distributed prior for substitution rate with a mean of 0.018 substitutions/site/Ma for mammals (40), 0.0105 substitutions/site/Ma for birds and reptiles (41) and 0.010 substitutions/site/Ma for amphibians (42), and a standard deviation of 0.005. All trees were time-calibrated using an uncorrelated lognormal relaxed clock model. In each species, the analysis was run 20 million generations with a sampling frequency of 2000, discarding the first 20% as burn-in. Further, phylogeographic clades were cross-checked using the GMYC method implemented in the "splits" R package (14). We used ultrametric tree from BEAST was used as the input for GMYC estimation, and applied both single- and multiple-thresholds for delimiting species, and we only considered the more conservative delimitation. In addition to BEAST, we also used BPP v3.4 (16) was also used to estimate the divergence time. We set the gamma prior on the population size parameter θ according to empirically estimated Watterson's θ summary statistic (43). Because of limited information for the divergence time τ, we determined its gamma prior by running preliminary runs in BPP to compare a deep divergence scenario with $\tau \sim$ G (2, 200) and a shallow divergence scenario with $\tau \sim$ G (2, 2000). The scenario with converged MCMC chains was chosen for each run. BPP analyses were run for 100,000 generations following a burn-in of 10,000 with a sampling frequency of 5. The convergence of τ and q parameters were examined in Tracer 1.6 (44), and estimated τ was converted to absolute time following Burgess & Yang (45) with the mean mutation rate of each species.

Detecting community-wide phylogeographic concordance

On our empirical data, we ran three independent MCMC chains for each river-specific analysis as well as the all-in-one analysis to verify convergence among the MCMC chains; 12 FBC runs were conducted in total. For each analysis, we used the following settings: (i) we selected the value of the Dirichlet process concentration prior to place approximately 50% of the prior

probability on the maximum number of divergence events using dpprobs program of the ecoevolity package (46); (ii) a gamma distribution (shape = 2.0, scale = 0.005) as the prior for population size, which is expected to be broad enough to cover the population sizes of studied species; (iii) a global set of mutation rate (μ) as 0.02/site/Ma and a scaler for individual clade-pairs was applied via their mutation rate relative to the global setting. All the other parameters were set as default (i.e. exponential distribution of event time prior with a rate of 100, auto optimization of operator setting with delay value of 1000). We used 150,000 generations for MCMC with a sampling frequency of 50, the convergence of MCMC chains were checked using Tracer (44).

For the FBC analysis with all the clade pair, we expected an over-estimated number of co-divergences. Applying a temporal "buffer" between pulses of co-divergences would filter the noise when large numbers of clade-pairs are submitted to ABC computation (47), but is not available with the current version of FBC. Hence, to investigated whether co-divergence on the temporal scale corresponds to co-divergence on the spatial scale, we extracted the posterior distribution of time estimates for each clade pair and calculated overlaps between the distributions. This gives a measure of how likely two clade-pairs have similar divergence time, more quantitative then directly using the FBC estimated co-divergence events. The FBC analyses for each riverine barrier were conducted with similar setting.

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Table 1 – FBC results at three rivers

	H1 - Asynchronous	**H2 - Synchronous**	**H3 - Partial synchronous**	
	Best events (Ψ>3)	**Best events (Ψ=1)**	**Best model**	**Best events**
Salween	cumulative PP (Ψ>3) = 0.015; 2lnBF* = 4.19	PP = 0.08; 2lnBF > 22.72	Ψ = 2 (PP = 0.76; 2lnBF > 30.02)	Ψ = 2 (PP = 0.91; 2lnBF = 23.55)
Mekong	cumulative PP (Ψ>3) ≈ 0; 2lnBF* < 6.49	PP < 0.0004; 2lnBF < 0	**Ψ = 3 (PP = 0.48; 2lnBF > 27.49)**	**Ψ = 2 (PP = 0.52; 2lnBF > 27.82)**
Yangtze	cumulative PP (Ψ>3) ≈ 0; 2lnBF* < -2.62	PP <0.001; 2lnBF < -2.62	Ψ = 3 (PP = 0.55; 2lnBF > 28)	Ψ = 3 (PP = 0.55; 2lnBF = 18.28)

* denotes the highest 2lnBF value among all Ψ>3 events; Bold characters indicates the best model and best events estimated in the Mekong scenario shows different numbers of divergence.

Figure 1. Map illustrating the main rivers and topography of the Mountains of Southwest China (MSWC). Colored symbols represent the geographic location of the samples. Purple triangle, orange square, and cyan circle denote samples of mammals, amphibians and reptiles, birds, respectively. Cyan patches show the maximum extent of glaciation during the Last Glacial, according to Owen and Dortch (2014).

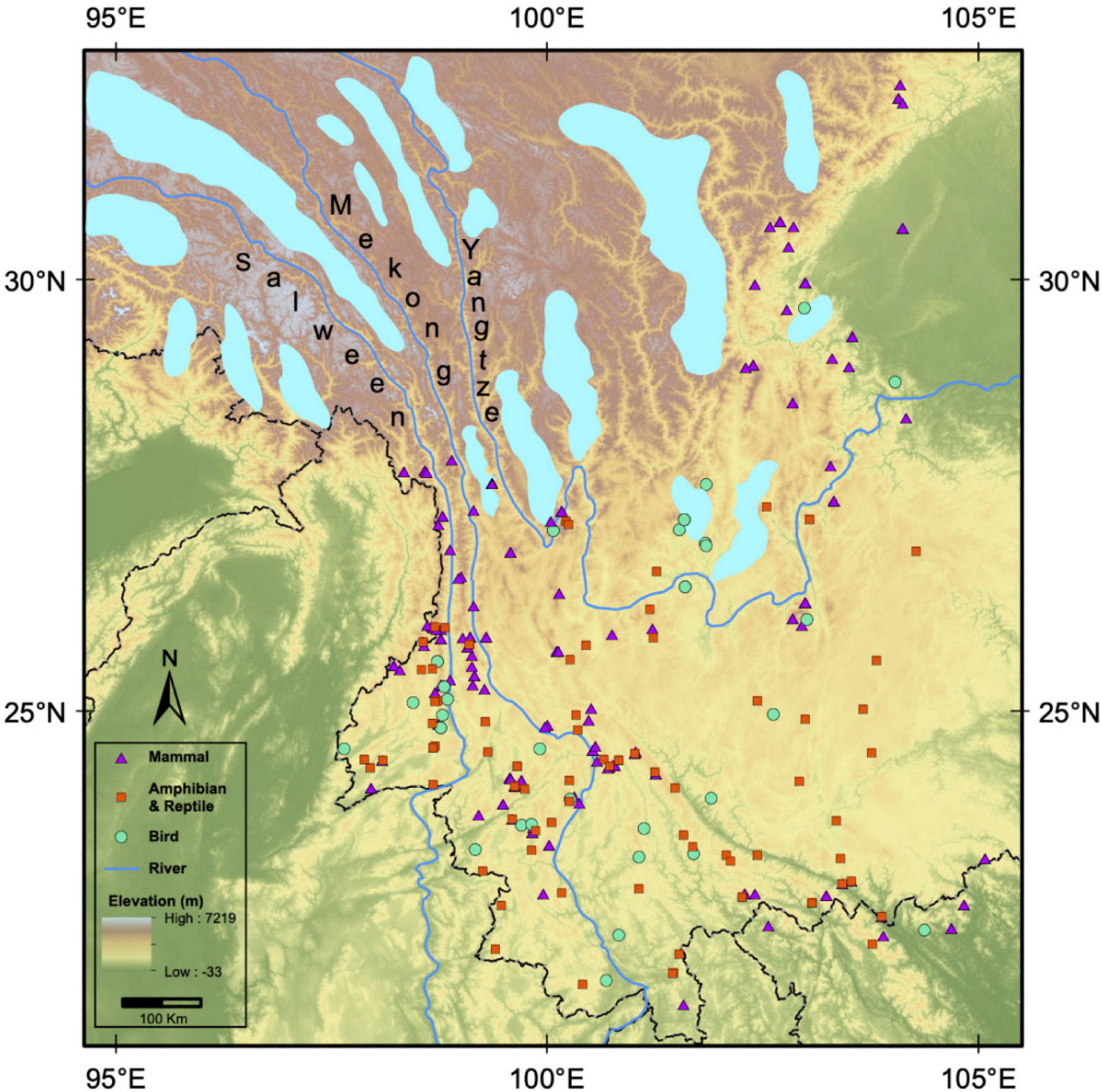
Figure 2. Testing comparative phylogeographic hypotheses among species with spatially concordant phylogeographic structure. The pairs of clades with a phylogeographic break at each river (the Salween, Mekong, and Yangtze) were identified, and hypotheses H1–H3 were tested using the full-likelihood Bayesian computation method. Different symbol shape represents different species; the within-species clades bounded by rivers are represented as contrasting colors.

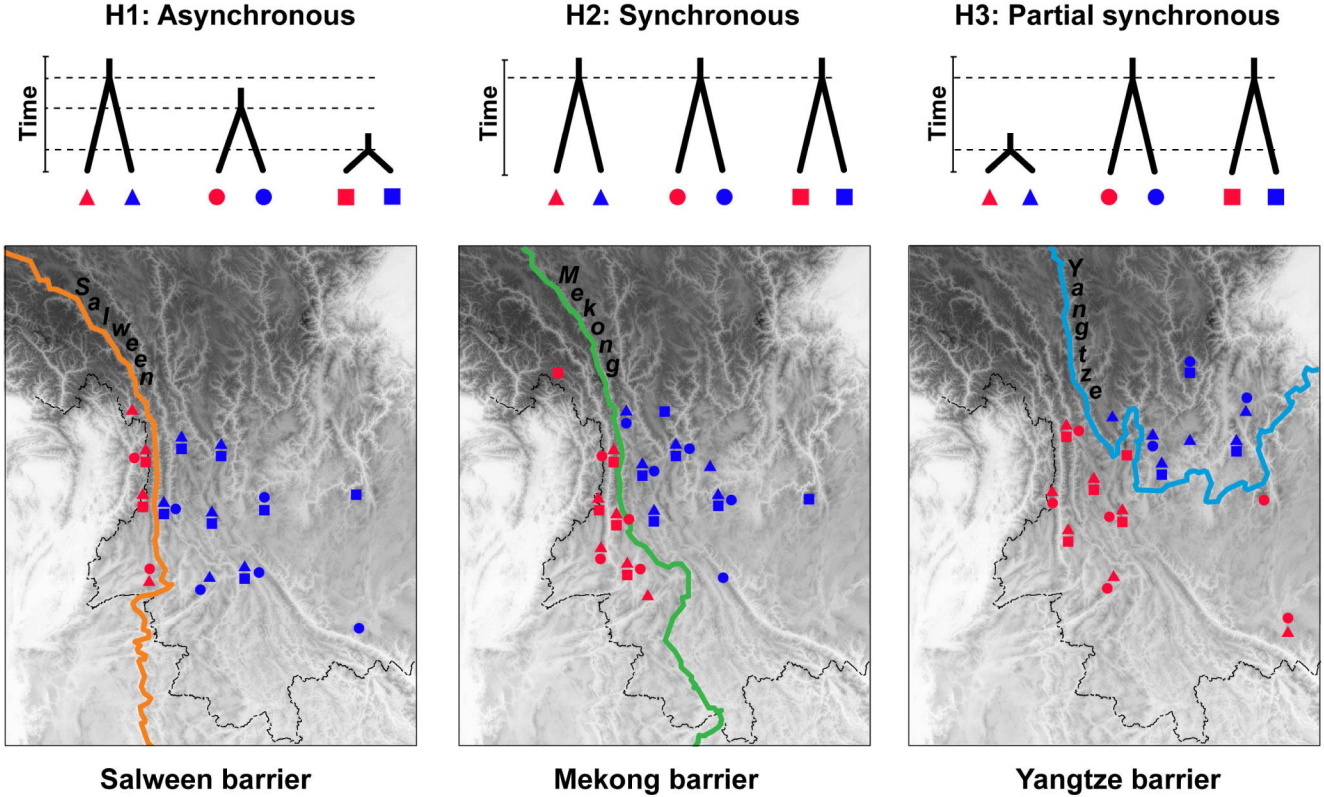
Figure 3. Divergence time (with mean and 95% credible intervals) between phylogeographic clades in 33 pairs of clades across riverine barriers. The time was estimated in BPP and divided by the mutation rate to convert into real-time. Squares, solid circles and triangles refer to amphibians and reptiles, birds, and mammals, respectively. Colors represent the isolation rivers. Orange, green, and blue represent species isolated by the Salween, Mekong, and Yangtze Rivers, respectively. The dashed line indicates the boundary of Early and Mid-Pleistocene. The bottom plot shows the record of Chinese Loess Sequence in the Pleistocene, where peaks represent Glaciations.

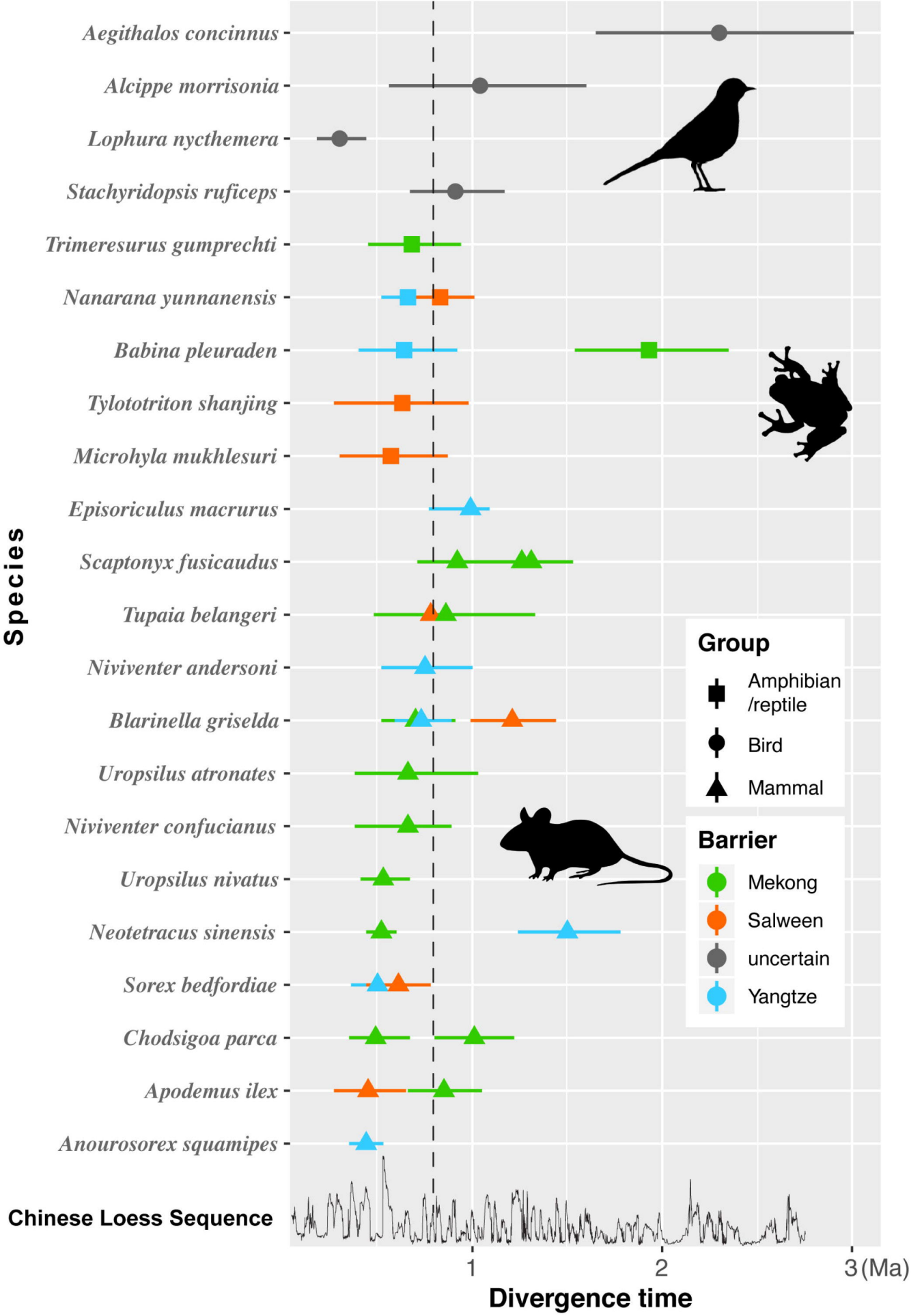
Figure 4. Testing phylogeographic synchronization using the full-likelihood Bayesian computation method at each river. (a), (c), (e) shows the approximate marginal posterior densities of divergence time for each clade pair. (b), (d), (f) shows the prior (light bars) and the posterior (dark bars) probabilities of the numbers of co-divergence events. The numbers above each bar denote the Bayes factor.

Figure 5. Putative mechanism for the community-wide phylogeographic diversity of MSWC.

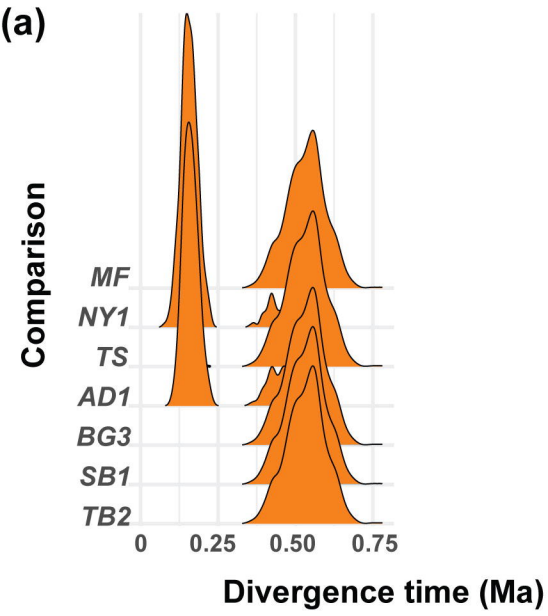
During drastic glacial cycles, phylogeographic divergence of montane species were intensively generated via dispersal to track their climate niche in lower and/or southern suitable habitats (i.e. refugia, marked with red orange patches); direction of dispersal could either along (orange arrow) or cross (red arrows) river barrier. Within mild glacial cycles, the environmental pressure is not harsh enough to promote cross-river dispersal, species could track climatic niche additionally using elevatioanl gradients (green arrows); the phylogeographic divergence formed in drastic glaciations could primarily preserved during this period of time.

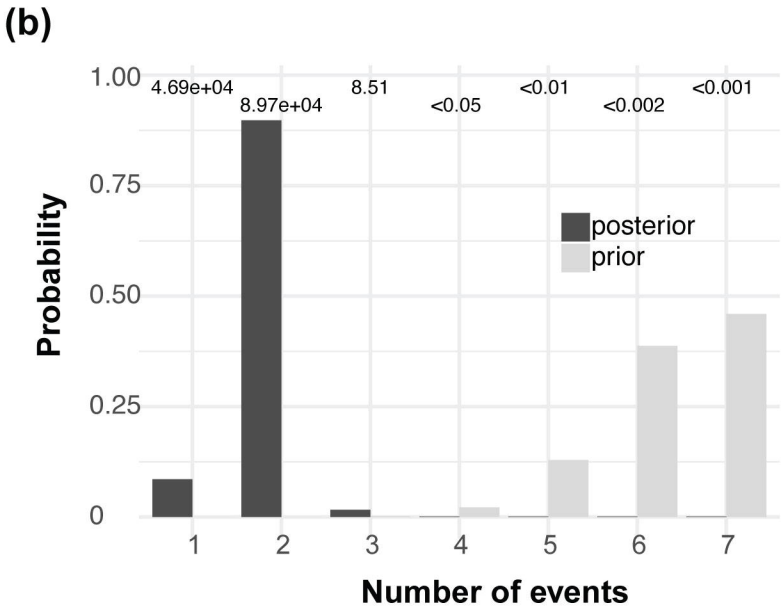

95°E
100°E
105°E
30°N
25°N
Salween
Mekong
Yangtze
N
Mammal
Amphibian & Reptile
Bird
River
Elevation (m)
High : 7219
Low : -33
100 Km


H1: Asynchronous
H2: Synchronous
H3: Partial synchronous
Time
Time
Time
Salween
Mekong
Yangtze
Salween barrier
Mekong barrier
Yangtze barrier

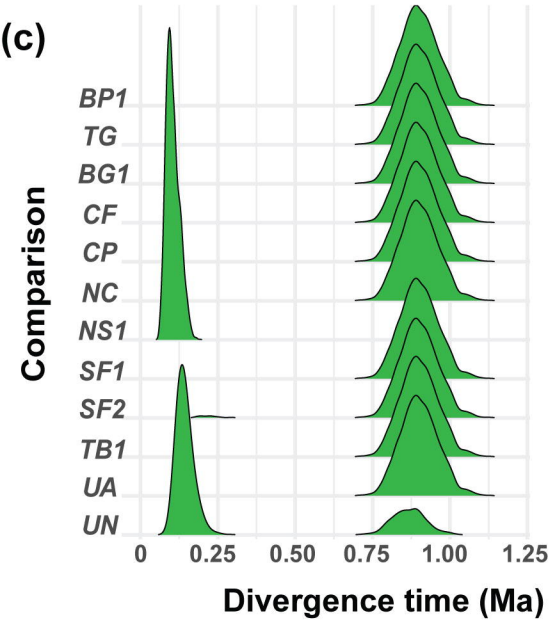

Aegithalos concinnus
Alcippe morrisonia
Lophura nycthemera
Stachyridopsis ruficeps
Trimeresurus gumprechti
Nanarana yunnanensis
Babina pleuraden
Tylototriton shanjing
Microhyla mukhlesuri
Episoriculus macrurus
Scaptonyx fusicaudus
Tupaia belangeri
Niviventer andersoni
Blarinella griselda
Uropsilus atronates
Niviventer confucianus
Uropsilus nivatus
Neotetracus sinensis
Sorex bedfordiae
Chodsigoa parca
Apodemus ilex
Anourosorex squamipes
Species
Chinese Loess Sequence
1
2
3 (Ma)
Divergence time
Group
Amphibian /reptile
Bird
Mammal
Barrier
Mekong
Salween
uncertain
Yangtze

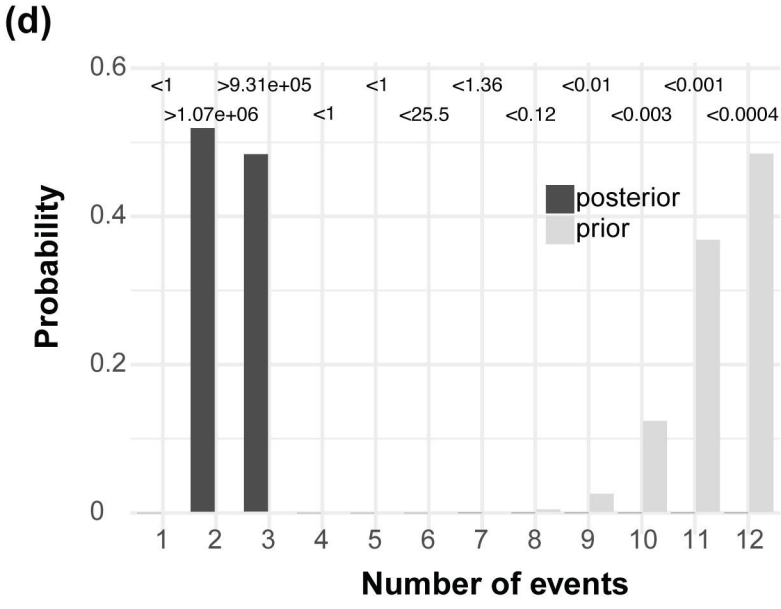
Salween barrier



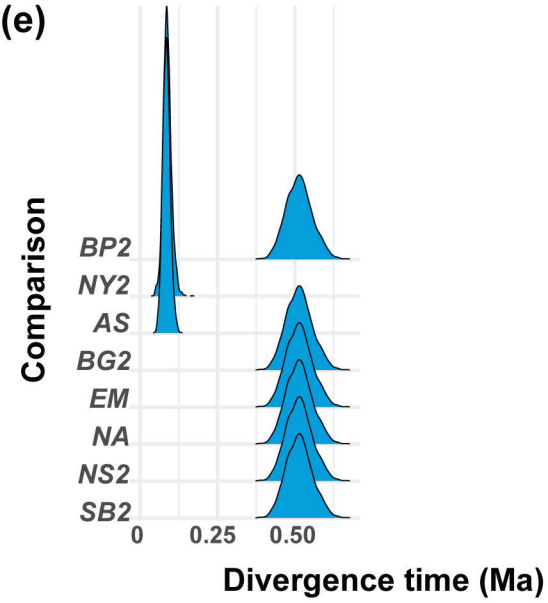


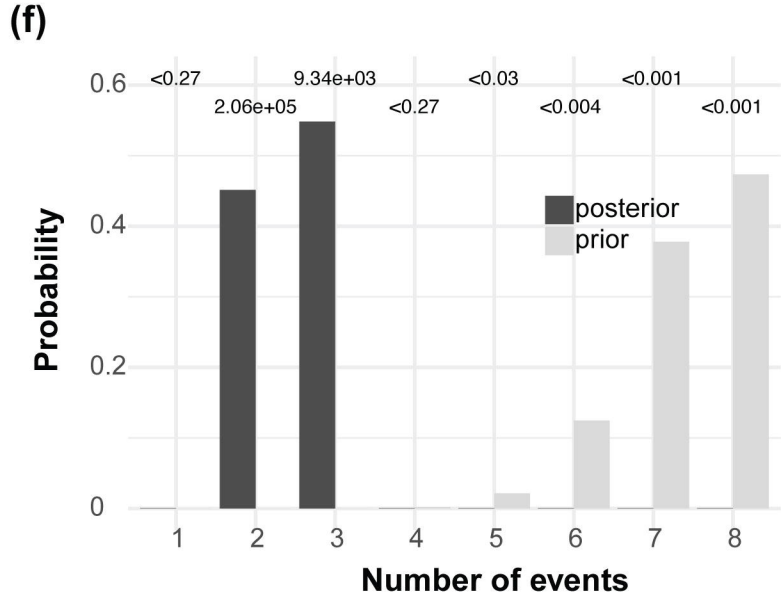
Mekong barrier

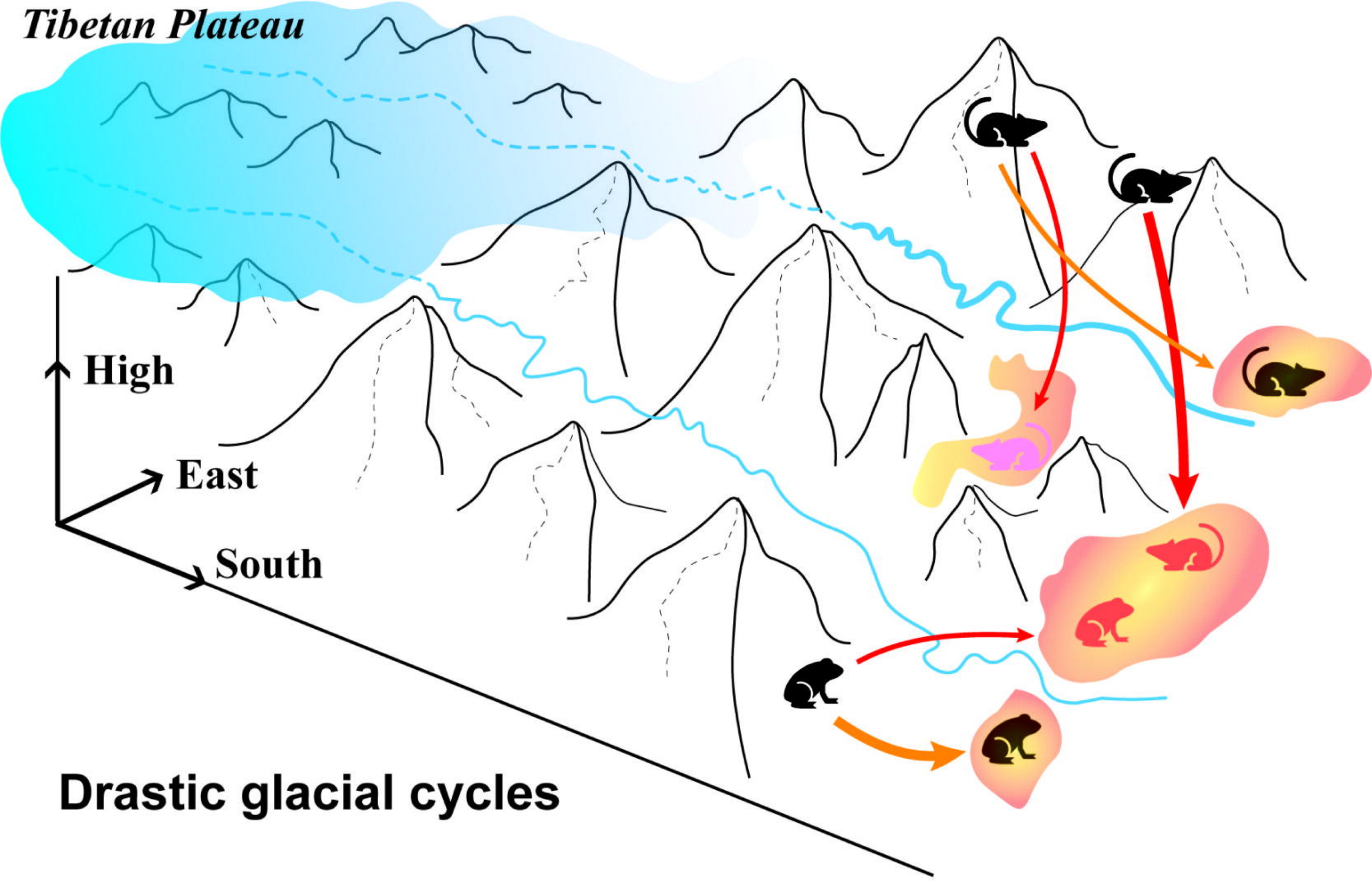


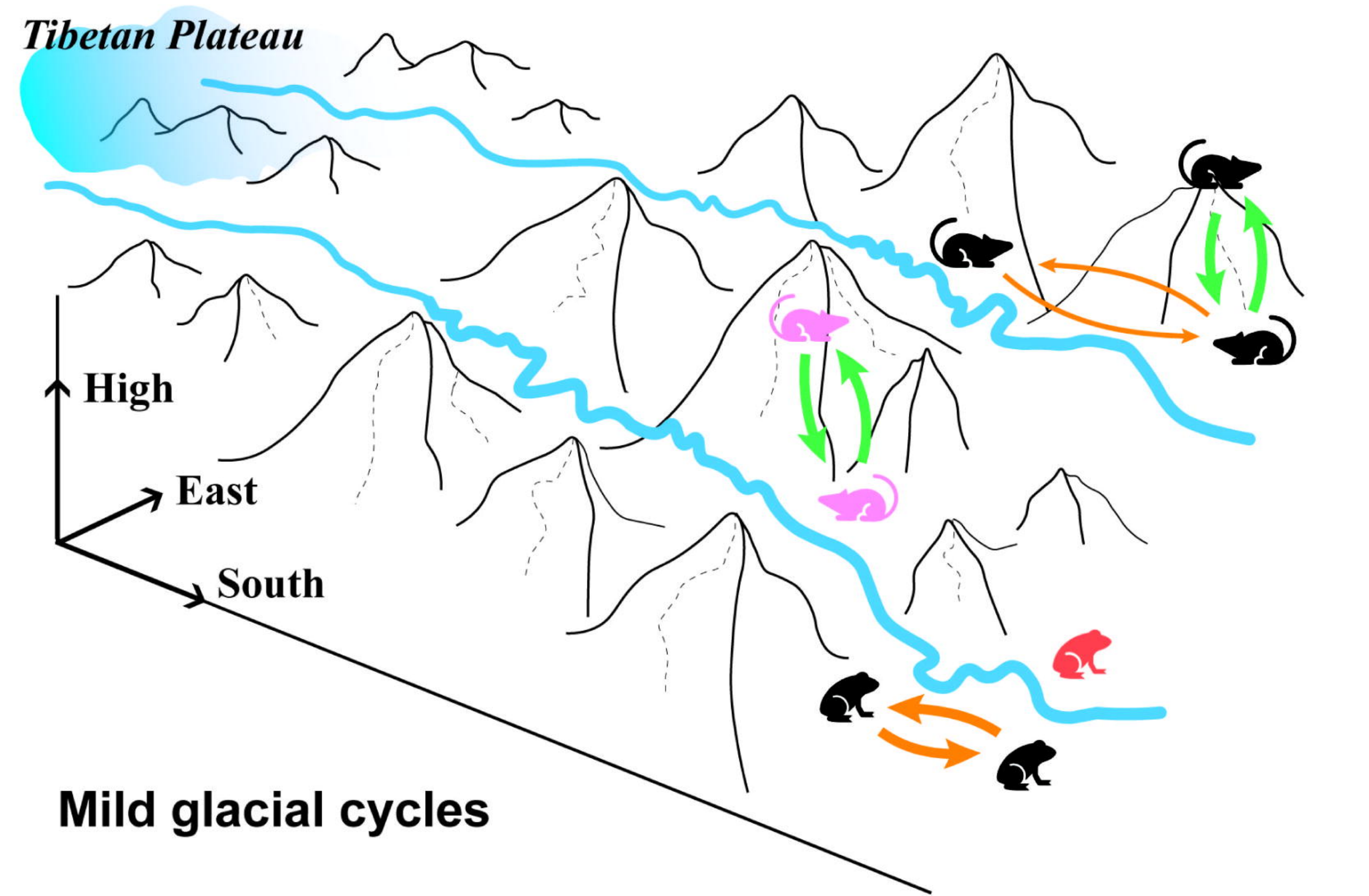


Yangtze barrier






Tibetan Plateau
High
East
South
Drastic glacial cycles


Tibetan Plateau
High
East
South
Mild glacial cycles